

Evolution of Sex Differences in Spatial Cognition

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ABSTRACT Psychological research has now clearly demonstrated that there is a significant difference between men and women in their performance on certain spatial tasks. Evidence further suggests that this difference has a neurological basis. This hypothesis is well enough established to have inspired several additional hypotheses concerning the evolutionary origin of the difference, including hypotheses emphasizing male hunting, female foraging, and male reproductive strategy. In this article we examine these hypotheses by placing them against the evidence for the neurological basis for the sex difference and the archaeological evidence for the evolution of spatial thinking in general. Given the probable source of the neurological difference in the timing of fetal testosterone, hypotheses that emphasize selection for female cognitive abilities are handicapped from the start. The hypotheses favoring male hunting and male reproductive strategy stumble when evaluated in light of the timing of the evolution of spatial cognition; archaeological evidence for the proposed selective behaviors and for the spatial abilities in question (e.g., mental rotation) do not correspond in a way that would permit a link between them. We conclude that none of the proposed adaptationist hypotheses fit the evidence as it currently exists, and that the modern sex difference in spatial cognition is almost certainly an evolutionary by-product of selection for optimal rates of fetal development. © 1996 Wiley-Liss, Inc.

The psychological literature has clearly documented sex differences in cognitive ability. Meta-analyses of scores of individual research projects have confirmed sex differences in aggression, verbal ability, quantitative ability, and spatial ability, to mention only the most salient and reliable results. These differences are just that—differences. The results of the meta-analyses and the experiments themselves do not require any judgment of better or worse in a more general sense. Women (and girls) perform better on some experimental tasks and men (and boys) on others. Moreover, while these differences can be identified in carefully controlled experimental situations, it is not yet clear the degree to which these differences influence the day-to-day lives of adult men and women (but see Benbow, 1988, and Geary, 1996, with commentaries).

The most reliable and largest differences in cognitive ability have been identified in the domain of spatial cognition (Halpern, 1992; Linn and Peterson, 1986). Indeed, statistical measures of the “effect size” of performance differences are higher for certain spatial tasks than for any other cognitive differences.¹ Spatial cognition is not, however, a unitary ability, but consists of at least four separate categories.² These are spatial perception, mental rotation, spatial visualization, and spatiotemporal ability.

Most tests of *spatial perception* require the

¹For example, effect size (*d*) for the Vandenburg version of the Shepard-Metzger mental rotation test was 0.94, or almost 1 SD (Linn and Peterson, 1986:73).

²Multivariate factor analysis of spatial abilities generally discriminates three orthogonal factors; the fourth is spatiotemporal ability (Halpern, 1992).

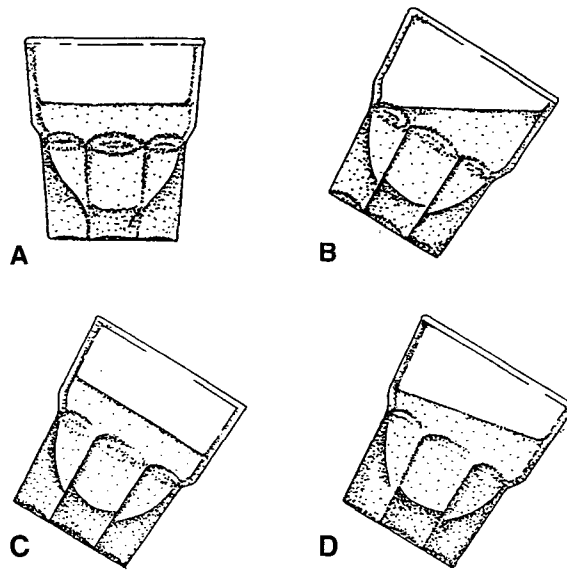


Fig. 1. In Piaget's water level test, the subject is shown a drawing of a glass of water (A) and asked to draw the water level if the glass were tilted. A correct drawing (B) depends on the ability known as "frame independence," which is an aspect of spatial perception. C and D are common errors.

subject to identify the horizontal or vertical within a distracting frame. Perhaps the most well-known example is Piaget's Water Level Task, in which the subject is asked to predict, by drawing, what the water level of a drinking glass will be when it is tilted (Fig. 1). Reliably, more males will draw the level at or close to horizontal; this result has always been especially provocative because, presumably, all Western men and women have extensive experience with drinking glasses. *Mental rotation* tests typically require the subject to view a complex figure and then pick from several optional figures the one that is a rotated view of the original (Fig. 2). As mentioned above, differences in performance on this test provide some of the largest effect sizes in the literature. Tests of *spatial visualization* require subjects to pick simple example figures out of a complex background (embedded figures test) (Fig. 3). Effect sizes of sex differences are lower for these tests than the previous two. Tests of *spatiotemporal ability* commonly test the ability of the subject to predict the time of arrival of a moving object at a designated point (Fig. 4). The inclusion of movement in these tests distinguishes them from the

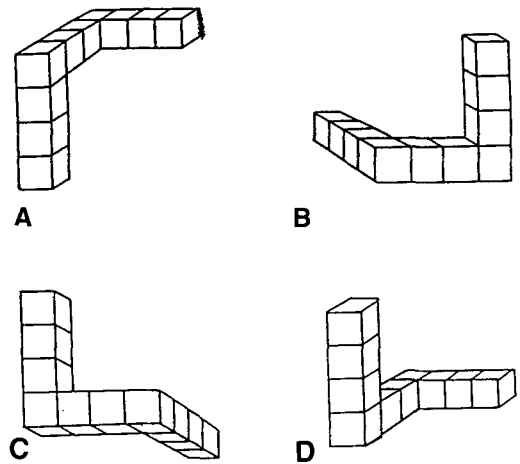


Fig. 2. An example of a test of mental rotation. The subject is asked to pick the example that is a rotated version of A. C is correct.

other abilities, but there is also clearly a spatial component. Moreover, like the others, there is a significant difference in the performance of men and women.

While the experimental results indicate that there is a measurable difference in performance, they do not as clearly delineate

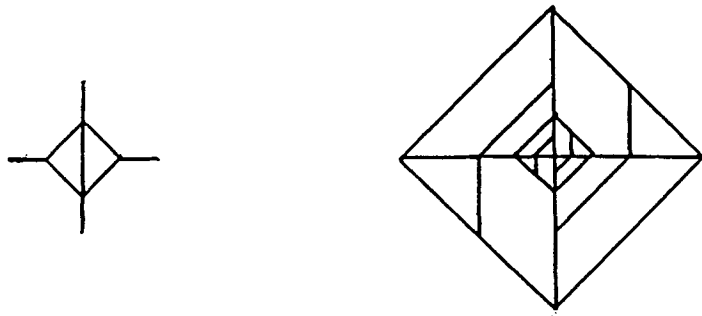


Fig. 3. An example of an embedded figures test, which is a test of spatial visualization. The subject is asked to identify the simpler drawing within the complex drawing.

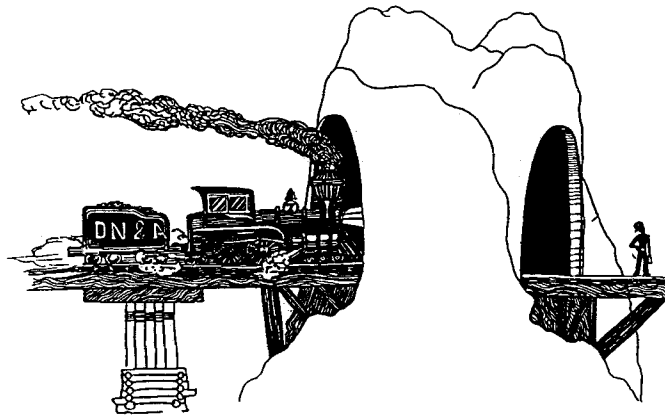


Fig. 4. In time to arrival experiments, subjects are asked to predict the "time to arrival" of a moving object that disappears from direct view.

the underlying cognitive basis. Not only do there appear to be several kinds of spatial thinking (as identified through multivariate analyses), other cognitive mechanisms affect performance. Warrick and Naglieri (1993), for example, have shown that girls excel at cognitive tasks that tap into attention and planning, while boys excel on tasks that rely on "simultaneous processing," which is the ability to survey elements and relate them to one another (p. 694). They go on to suggest that the female advantage in attention and planning may underlie the difference in verbal abilities, while the male advantage in simultaneous processing may underlie the difference in spatial tasks. Some of the performance differences may relate to problem-

solving strategies. Gallagher and De Lisi (1994) have argued that the gender difference in performance on the Scholastic Aptitude Test in mathematics results from differences in problem-solving strategy; females are more likely than males to use remembered conventions, and males more likely to use unconventional approaches. Personality also may play a role. In their study of gender differences in judging time of arrival of moving objects, Schiff and Oldak (1990) found that performance correlated with risk taking—individuals less inclined to take risks underestimated time of arrival, especially when motion was directed toward the observer. Our point here is not to suggest that spatial cognition is simply a epiphenomenon

of other cognitive systems, but to emphasize that performance on spatial tasks does not measure a single, simply defined cognitive ability. Moreover, to the degree that there is spatial cognition, it is not necessary that all tested behaviors rely on it to the same extent. To cite a purely hypothetical example, attentional factors may play a more important role in spatial perception than they do in mental rotation, which would influence the effect size of the gender difference.

The most robust gender difference shows up in the test that appears least relevant to the everyday world of human experience. The ability to rotate mentally a complex three-dimensional object (usually presented in two dimensions) has few practical applications. Spatial perception and spatial visualization, as usually tested, are slightly less esoteric; the ability to "see past" extraneous distractions (frame dependency) and pick patterns out of complex backgrounds might be useful skills. Spatiotemporal ability is perhaps the one with the most easily imagined benefits—dodging traffic comes to mind—but it is also the one in which spatial cognition per se plays the least clearly defined role. Alyman and Peters (1993) have called attention to this problem. "[T]he kinds of tests that have been used in order to assess sex differences in spatial behavior do not only contain various and differently defined aspects of 'spatiality,' but they are abstract representations of 'real life' behavior" (p. 731). To get around the problem they devised a series of practical spatial tasks (such as estimating crowd size and estimating one's own body length on the floor). Here the results were not as clear cut as those on more abstract tasks, and Alyman and Peters found few significant gender differences. "In all, the data emphasize the fact that sex differences are not by any means seen in all spatial tasks. The claim that 'males excel in spatial tasks' misrepresents the situation and must give way to the more conservative statement that males perform better than females on *some* spatial tasks" (Alyman and Peters, 1993:744).

In sum, the experimental evidence does indicate that there is a real difference between males and females in their performance on tests of spatial ability. It is not

clear just what cognitive ability underpins the difference, or whether there are several spatial skills or only one which is differentially applied in the various tests. Nor is it clear that this cognitive difference has any practical consequences.³ Despite these uncertainties, the sex difference in spatial cognition has entered the popular and semi-popular literature, where it has been co-opted for social and political agendas of various kinds (e.g., Tavris, 1992). Because of the potential volatility of the general issue of cognitive sex differences, we feel that it is essential to examine this most salient difference very carefully. As evolutionary anthropologists, we believe that the significance of this modern cognitive difference can only be understood in a context of evolutionary theory and the actual evidence of human evolution, in particular the archaeological evidence for past human spatial abilities. In the following essay we will first present four hypotheses for the evolution of sex differences in spatial cognition, after which we will review the evidence for its neurological basis, and summarize important developments in the archaeological record. We conclude by identifying the hypothesis that best fits the neurological and archaeological evidence.

FOUR ALTERNATIVE EVOLUTIONARY HYPOTHESES

When examining the evolutionary basis of a trait it is crucial to realize that the trait's mere existence does not mean that it was favored by natural selection. While some aspects of phenotypes are adaptations, others may be the products of genetic drift or pleiotropic genes, or simply the by-products or side effects of adaptations (Gould and Lewontin, 1979). Hence, an evolutionary analysis does not simply attempt to determine the evolutionary function of a trait, it attempts to determine whether the trait is even an adaptation.

Even if one successfully avoids the natu-

³However, the U.S. Air Force has supported research into cognitive sex differences in spatial ability, presumably because of its relevance to flight training. See, for example, Tirre and Rouff (1994).

realistic fallacy of associating adaptations with moral values, it is often difficult to determine whether an aspect of a phenotype is itself an adaptation. This is because demonstrating that a trait or character increases an individual's inclusive fitness is not sufficient evidence that the trait is an adaptation. "To say that a given beneficial effect of a character is the function, or a function, of that character is to say that the character was molded by natural selection to produce that effect" (Symons, 1979:10). Hence, measuring current reproductive success (see Caro and Borgerhoff Mulder, 1987) cannot demonstrate that a trait is an adaptation because there is the possibility that the trait may not have had a beneficial effect in ancestral environments or "the trait, although once adaptive under conditions that no longer exist, is currently maladaptive" (Alcock, 1983:11; see also Symons, 1989). Indeed, making a plausible argument that the trait would have had a positive effect on inclusive fitness in the "natural" environments of ancestral populations is still insufficient because the trait "may not have a genetic basis . . . [or] variation in reproductive success may actually be caused by variation in some other character with which the character is correlated" (Symons, 1979:11). Hence, "[t]he demonstration of a benefit is neither necessary nor sufficient in the demonstration of function, although it may sometimes provide insight not otherwise obtainable. It is both necessary and sufficient to show that the process is designed to serve the function" (Williams, 1966:209).

Nearly 30 years ago, Williams (1966) proposed the following criteria for determining if a trait has been designed by natural selection.⁴ In addition to cross-species comparisons, a "plausible demonstration of design" consists of demonstrating that a trait accomplishes its alleged function with "sufficient precision, economy, and efficiency, etc." (Williams, 1966:254, 10; see also Crawford and Galdikas, 1986; Curio, 1973; Dewsbury, 1980; Palmer, 1989; Symons, 1980, 1987).

Williams also warned that "adaptation is a special and onerous concept that should be used only where it is really necessary" (Williams, 1966:4–5). Although some researchers have overlooked this warning in their zeal to find adaptive explanations, the "onerous" nature of adaptations remains widely accepted. Indeed, Symons points out that "[a] function can be distinguished from an incidental effect insofar as it is produced with sufficient precision, economy, and efficiency to rule out chance as an adequate explanation of its existence" (Symons, 1979:11). Hence, according to the doctrine of parsimony, "if an effect can be explained adequately as the result of physical laws or as the fortuitous byproduct of an adaptation, it should not be called a function" (Symons, 1979:11).

Losco has pointed out that unjustified claims of adaptation are particularly likely when the proximate causes of a trait are ignored: "... insufficient attention to proximate concerns may result in a misreading of the forces at work in the selection process. Researchers who concentrate exclusively on ultimate function run the risk of cataloguing behaviors as 'adapted' which may instead be by-products or secondary effects of other adaptations" (Losco, 1981:336; see also Gould, 1987; Gould and Lewontin, 1979). In light of the need to assume that a trait is merely a by-product until it is demonstrated to be an adaptation, it is crucial to examine the proximate mechanisms producing a trait: "The decision as to the purpose of a mechanism must be based on an *examination of the machinery* and an argument as to the appropriateness of the means to the end" (Williams, 1966:12; emphasis added). Several proposed functions of the previously described male/female differences in cognitive spatial abilities will now be examined to see if the available evidence shows sufficient indications of design for the differing abilities to be considered adaptations.

ADAPTATIONIST THEORIES OF SPATIAL SEX DIFFERENCES

There are three basic types of adaptationist explanations for the sex differences observable in spatial cognition. Two propose

⁴Although Williams' critique of "group selection" is currently the source of considerable controversy among evolutionary biologists (see Wilson and Sober, 1994), his criteria for determining adaptation, at any level of selection, remain widely accepted.

that "sex differences in spatial abilities originated in human evolution as a function of division of labor" (Eals and Silverman, 1994:95; see also Silverman and Eals, 1992) by way of selection for male-biased abilities in hunting and/or female-biased abilities in foraging for plants and small animals. Although both of these hypotheses may be right or wrong, the validity of one does not determine the validity of the other and we will examine them separately. The third adaptationist explanation (Gaulin and Fitzgerald, 1986; Gaulin and Hoffman, 1988) is based on the broader basis of differences in male and female reproductive strategies that may include, but are not restricted to, the division of labor.

The argument that male spatial abilities are somehow tied to hunting abilities has been put forth by Jardine and Martin (1983), Kolakowski and Malina (1974), O'Brien (1981), and Calvin (1993). In essence, this hypothesis argues that activities associated with the hunt, in particular the effective use of projectiles, selected for male-specific spatial abilities. The universality of this cognitive sex difference and its basis in hormonal differences lend some initial credence to this hypothesis. However, to be persuasive, the hypothesis must explain how the proximate developmental connection between hormones and a cognitive sex difference could have been selected by hunting. Unfortunately for the hypothesis, this connection is based in laterality of brain function, and it is far from certain that lateralization itself evolved to produce any differences in cognitive abilities, let alone abilities used in hunting (see below). It is also necessary that the hypothesis provide evidence that the specific abilities "fit" the selective pressures (e.g., mental rotation helps hunting), and that the selective pressures were present when the abilities appeared. In this case, the appearance of these abilities must coincide with the advent of hunting as a major human subsistence strategy.

Eals and Silverman (1994) have emphasized female abilities. They propose that female spatial abilities are an adaptation designed by the selective pressures related to foraging: "Successful foraging . . . would require locating food sources within complex

arrays of vegetation and finding them again in ensuing growing seasons" (Eals and Silverman, 1994:96). Such pressures, according to Silverman and Eals (1992:489), would select for "the recognition and recall of spatial configurations of objects: that is, the capacity to rapidly learn and remember the contents of object arrays and the spatial relationships of the objects to one another. Foraging success would also be increased by peripheral perception and incidental memory for objects and their locations, inasmuch as this would allow one to assimilate such information non-purposively, while walking about or carrying out other tasks."

In addition to demonstrating that these selective pressures coincided with the advent of the appropriate spatial abilities, the hypothesis must demonstrate that female spatial advantages (spatial visualization in particular) are precisely linked to the selective pressures of foraging. Such a linkage appears to be problematic because many of the tests suggest that females' greater object recall ability might be related to the greater *verbal* recall ability (Maccoby and Jacklin, 1974; Burstien et al., 1980; Eals and Silverman, 1994).

Perhaps the most plausible adaptationist explanation is the hypothesis that the greater spatial abilities of men were selected because "the navigational demands on [ancestral] males exceed[ed] those on [ancestral] females" (Gaulin and Hoffman, 1988:132). Although hunting activities might have been part of the reason ancestral males may have had larger home ranges in humans, Gaulin and Hoffman suggest a broader function of spatial abilities related to the different reproductive strategies of males and females in many mammals. Hence, their explanation rests on the more general assumption that ancestral human males had larger ranges "*in order* that they may increase their access to potential mates" (1988:144; emphasis in original).

Gaulin and Hoffman support their hypothesis with the following types of evidence. First, there appears to be a cross-species correlation between male-biased spatial abilities and nonmigrating polygynous species (Gaulin and FitzGerald, 1986). Hence, the male-biased spatial abilities in humans are

consistent with the fact that humans are a mildly polygynous species. Second, they argue that the sex differences in spatial ability occur at precisely the right point in development to influence reproductive tactics: "sex differences in spatial ability become much more pronounced at adolescence and then decrease in middle age" (1988:137); "[hence,] sex differences in spatial ability are maximal just after the attainment of sexual maturity [which] is consistent with the interpretation that spatial ability is a reproductive tactic of differential value to males and females" (1988:133). Third, the available evidence on male and female ranging behavior among contemporary humans suggests that males often have a larger home range (1988). Finally, and perhaps most importantly, Gaulin and Hoffman suggest that the male-biased spatial abilities are efficiently designed to meet the precise function of navigation in a way that is analogous to the way the olfactory system is designed for the function of monitoring an abundance of various volatile compounds: "In the same sense, spatial ability is intimately linked to the maintenance of a clear image of the spatial organization of the environment and a sense of one's own position in that environment" (1988:131).

SEX DIFFERENCES AS A BY-PRODUCT OF THE TIMING OF PRENATAL HORMONES

If, as suggested by Falk (1987), major male/female differences in brain asymmetries and laterality of function are the result of developmental timing related to growth of the hemispheres and the ambient levels of fetal testosterone, then male/female differences in cognitive abilities (to the extent they really exist) can be explained in much simpler terms. While not downplaying the importance of natural selection in human evolution, we find the major adaptationist explanations for the development of human male/female differences in cognitive abilities to be less than satisfactory.

A more parsimonious explanation for adult human male/female cognitive differences is that they are the result of developmental factors. For example, selection for earlier fetal maturation could result in fetal

exposure to testosterone at earlier times, which would influence the hemispheric growth that was also programmed to occur at that time. The result would be a change in the expression of male/female cognitive abilities, but only as a by-product of the timing of fetal maturation.

Since it appears that increased maternal protein intake during pregnancy increases the rate of fetal maturation (Tierson et al., 1986; Susser and Stein, 1980), a change in diet (by increasing protein intake) over the evolutionary development of the human species could be responsible for earlier fetal maturation, thereby providing the selective mechanism which results in more asymmetric development of the hemispheres of the brain.

A hypothesis emphasizing fetal or maternal viability would a priori be stronger than a hypothesis emphasizing cognitive abilities later in life; fetal and maternal viability are much more immediate to the question of reproductive success. Selection for maximum fetal viability would clearly play an important role in evolution, but selection for maternal viability may also have been important. For example, it is clear that the effect of testosterone may depend both on the level of the free hormone and on tissue sensitivity (Geschwind, 1987). Consequently, excessive testosterone effects may be obvious in some female fetuses in whom sensitivity is higher. Since tremendous differences exist in maternal levels of progesterone production during early pregnancy, and since higher levels of progesterone production usually correlate with increased levels of nausea and vomiting of pregnancy (Tierson et al., 1986; Tierson, 1991), selection might operate against increased amounts of nausea and vomiting in pregnancy, through a change in the timing of fetal development. This in turn could change the exposure of the fetus to the effects of testosterone, resulting in the differential development of the hemispheres of the brain. Again, any final adult male/female differences in cognitive abilities would simply be a by-product.

Of course, the action of nausea and vomiting of pregnancy is unclear. Maternal dietary cravings and aversions during preg-

nancy clearly affect consumption of food items for which cravings/aversions develop (Tierson et al., 1985). Dietary cravings and aversions during pregnancy are clearly related to nausea and vomiting of pregnancy. Many explanations of the development of these symptom complexes in humans point to their potential fetoprotective nature. For an excellent discussion of adaptive hypotheses for these complexes of symptoms, see Profet (1992). However, controversy exists regarding the adaptationist explanations for the development of nausea and vomiting of pregnancy. Any coincidental fetoprotective aspect may be the by-product of changes in fetal maturation rates (Tierson, in press). Additionally, the variability in hemispheric dominance among females and males separately, and between the sexes, could be increased dramatically if nausea/vomiting of pregnancy appreciably affected the amount of usable circulating testosterone during early fetal development.

A satisfactory evolutionary explanation for documented sex differences in spatial cognition must consist of more than a plausible evolutionary scenario. It must also account for all of the available evidence. We have found that the evolutionary scenarios proposed to date fail to consider adequately two major bodies of evidence: the neurological evidence for the ontogeny of the sex difference and the paleoanthropological evidence for the evolution of spatial abilities, including the evolutionary context of cognitive evolution.

ONTOGENY OF BRAIN ASYMMETRY AND LATERALITY OF FUNCTION

Vertebrate brains are asymmetrical; the right hemisphere is not a precise mirror of the left. Furthermore, the two halves do not contribute to vertebrate cognition in identical ways, something termed laterality of function. Asymmetry is most often used to refer to the anatomical differences between the hemispheres, while laterality is used to refer to functional differences. Sex differences in laterality and asymmetry appear to be the organic basis for the cognitive differences in spatial cognition (Halpern, 1992), and it is here that we must look for the proxi-

mate selective mechanism. What selected for the human sex differences in asymmetry and laterality?

The simplest theory of asymmetry and lateralization is that these patterns are largely a result of genetic determination. However, it has become clear that nongenetic factors can also have a dramatic effect. The most important of these nongenetic factors is fluctuation in the chemical environment of fetal development (Geschwind, 1987). Such chemical/hormonal influences can extend throughout infancy and into early childhood, and perhaps even throughout adult life.

EXTENT OF CEREBRAL ASYMMETRY AND LATERALIZATION AMONG VERTEBRATES

Cerebral asymmetry can best be understood as deviations from complete bisymmetry in the specializations of paired structures in the nervous systems of bisymmetric organisms (Hiscock and Kinsbourne, 1995). Most researchers understand bisymmetry to be an adaptation for motility, including bisymmetry of those parts of the central nervous system that control movement.

Until recently, the significance of brain asymmetries in nonhuman animals, especially as they related to human lateralization, was a topic that was hotly discussed. Even the existence of widespread brain asymmetries among many species of nonhuman animals was not well known. However, these differences in lateralization are now well recognized among many species including fish, reptiles, and birds (Hiscock and Kinsbourne, 1995; Braitenburg and Kemali, 1970). Domestic chicks, for example, have various asymmetries, and also demonstrate a hemispheric shift of control related to increasing familiarity in a manner similar to humans (Goldberg and Costa, 1981). This shift involves the right hemisphere for initial responses to novel situations, with a switch to the left hemisphere as behavioral patterns are developed (Hiscock and Kinsbourne, 1995). Asymmetries are widespread in rodents, including asymmetries of cortex, hippocampus, and amygdala. An excellent recent summary of the brain morphology asymmetries in rats can be found in Lewis

and Diamond (1995). Summaries of behavior asymmetries in rats, and the neurochemistry of such asymmetries, can be found in Hiscock and Kinsbourne (1995).

Numerous types of brain asymmetries have been documented for nonhuman primate species. Until recently, primates have been held up as an especially important link in our understanding of human lateralization. However, as our understanding of morphological asymmetries among nonprimates has increased, the relative importance of nonhuman primates—at least in terms of understanding the ontogeny of lateralization in humans—has decreased. Nonhuman primate lateralization remains of interest mainly because it is widespread (see Galaburda, 1995, for a summary of structural asymmetries among nonhuman primates), and because of “the genetic, neurologic and behavioral similarity” between nonhuman primates and humans (Hiscock and Kinsbourne, 1995:543). Asymmetries in sylvian fissures have been reported in baboons, orangutans, chimpanzees, and humans (Falk, 1978; Falk et al., 1990, 1991). Frontal asymmetries in favor of the left side have been reported in baboons and orangutans, while the right frontal lobe commonly predominates in humans (LeMay and Geschwind, 1975; Falk, 1978; Cheverud et al., 1990; Falk et al., 1990; Galaburda, 1995). Although it is clear that differential specialization of the cerebral hemispheres is common in nonhuman primates, the connection between this differential specialization of the hemispheres and performance lateralization is unclear at best (Hiscock and Kinsbourne, 1995).

Structural asymmetries in humans

The human brain is clearly asymmetric and demonstrates laterality of function (Galaburda et al., 1978; Geschwind and Levitsky, 1968; Steinmetz et al., 1991; Galaburda, 1995). Even during early fetal development the human brain displays asymmetries in structure (Geschwind, 1987), including hemispheric asymmetry in the orientation of the Sylvian fissure (LeMay and Culebras, 1972) and a larger left plenum temporale (Wada et al., 1975; Chi et al., 1977). However, even though the left hemisphere is signifi-

cantly different in function from the right, the structure and chemical constituency of both hemispheres are essentially the same in spite of the well known anatomical and histological asymmetries (including hemispherical differences in the distribution of certain neurochemicals or their receptors). However, all architectonic regions are to be found in both hemispheres (Galaburda, 1995). As stated by Galaburda: “. . . There are no cell types found in one hemisphere but not in the other. There is no known pattern of connections that appears to be specific to the dominant hemisphere. And, as far as has been determined, there are no physiologic properties in neurons of one hemisphere that are not present in the other. This leaves quantitative differences as the only difference between areas present in both hemispheres” (Galaburda, 1995:52).

This does not, of course, mean that quantitative differences are unimportant, and the importance of such quantitative differences should not be minimized. However, it does mean that any qualitative differences between the hemispheres are a product of a threshold effect tied to the relative sizes of component structures.

In any discussion of human brain asymmetry three important points must be considered: 1) the direction of the asymmetry, 2) populational variability in the direction of asymmetry, and 3) the degree of the asymmetry (Galaburda, 1995).

Direction of asymmetry refers to whether a particular structure of the brain is larger on the right or left side. Several neuroanatomic asymmetries have been noted in the human brain. One of the earliest reports of such asymmetry in the scientific literature is that of the plenum temporale (Geschwind and Levitsky, 1968). One interesting fact related to this is that, although about 65% of their sample population showed a longer left plenum temporale compared to only 11% displaying a longer right plenum temporale (both were equal in the remaining 24% of the sample), brains displaying a reversal of normal asymmetry look like mirror images of those with “normal” asymmetry (Galaburda, 1995). Such asymmetry also extends at least to Heschl’s gyrus, to the Sylvian fissure, to varied areas of the inferior frontal

area, and to gross anatomic asymmetry of the cerebral cortex.

Not only are gross anatomical asymmetries important, but asymmetries in regional cortical organization (including fluctuations in thickness of cortical layers, fluctuations in numbers of layers, variability in the size and shapes of neurons in the cortical layers, variability in the density of the neurons, and specific local arrangements of the neurons in clusters and columns) are important as well. Such asymmetries have been demonstrated in several cortical areas related to language function, including area Tpt, the angular gyrus and varied parts of Broca's area, among several others (Galaburda, 1995). One of the most general observations about brain asymmetries in humans is that the left hemisphere is larger in regions tied to linguistic capabilities and that the right hemisphere is larger in regions tied to visuo-spatial abilities. However, this pattern of hemispheric specialization is not always the case. A good summary of hemispheric dimorphism in humans can be found in Falk (1987).

The pattern of asymmetry just described is not universal. A relatively large proportion of the individuals in any population may display reversed asymmetry. For example, in areas related to language ability (the *plenum temporale*), approximately 70% of human brains display leftward asymmetry, while 10% show the reverse asymmetry (Galaburda, 1995). When such reversal of "normal" asymmetry does occur, the right hemisphere usually looks more like the typical left hemisphere, and vice versa.

The degree of asymmetry also can vary considerably. Asymmetry is a continuous variable, not a discrete one. Striking differences in the amount of asymmetry for the same feature can be seen in different individuals. This variability probably reflects the lack of a mechanism for keeping developments in the two hemispheres synchronous during growth and development; if maturation falls out of step, it remains out of step. Such a situation would be especially conducive to the development of asymmetry as a result of differential effects of the prenatal and postnatal environment on the two individual hemispheres.

Similar directional asymmetries appear to exist across populations, species, and even orders (for example, left hemisphere dominance for vocal communication in birds and primates). Can such "directional" asymmetries exist if they are simply the result of the lack of a mechanism for keeping development of the two hemispheres synchronized? First, similar selective forces could easily have affected such directional patterns among populations of the same species, or among species of the same genus. Additionally, there are only three possibilities when speaking of hemispheric dominance: left dominance, right dominance and left/right symmetry. What appears to be a direction in the pattern of hemispheric dominance might simply be a product of the limited number of possibilities and the human tendency to find a direction (whether it really exists or not).

There is also a sex difference in laterality. Females appear to be less lateralized than males; they are more likely than males to use both cerebral hemispheres when solving a task and to devote less neural space in the dominant hemisphere to a particular lateralized function. Language, for example, is a strongly left-lateralized function, but when speaking, females also employ the right hemisphere, certainly to a far greater degree than males. Males, on the other hand, are more lateralized, being more likely than females to focus neural activity in a single hemisphere while solving tasks. In language, males are more left-hemisphere dominant than females. One consequence of this appears to be a much higher incidence of dyslexia and stuttering in males than females; greater laterality is not necessarily a good thing. The male advantage in spatial reasoning appears to be tied to the greater laterality of male brains, in particular the greater reliance on the right hemisphere. While there is a clear sex difference in laterality of function, this is not manifested in gross differences in asymmetry, though male brains tend to have less pronounced left asymmetry. Male and female brains show the same basic asymmetric pattern. However, the difference in laterality almost certainly results from sex differences in the development of right and left hemispheres,

differences resulting from the timing of prenatal sex hormones (Halpern, 1992).

One of the factors that has the potential for producing variability in the degree of asymmetry is the level of sexual steroids during fetal development and the potential effect of differing levels of such hormones on the development of the left and right hemispheres. If the rate of development of the two hemispheres differed, then an increase in a particular hormone at any particular time would influence the growth of the two hemispheres differentially. The final effect, whether the left or right hemisphere would be retarded in growth compared to the other, would be influenced only by the timing of increases and decreases in specific hormone levels and the particular time when one or the other of the two hemispheres was programmed for growth. If the programmed times were different, then the hemispheres would be driven toward developing a specific asymmetry of structure.

CAUSES OF CEREBRAL ASYMMETRY

Even before birth, major asymmetries are present in the cerebral cortex. As Galaburda (1995:58) states, "the anatomic asymmetries that may underlie functional lateralization are fixed, at least in their gross design, before birth." Since the gross anatomy of the brain does not change significantly after birth, any patterns established before birth will be reflected later in life. Additionally, asymmetry is established early during corticogenesis, most likely as early as the time when neuroblast pools are being established on both sides of the midline of the neural tube (Galaburda, 1995; Geschwind and Galaburda, 1985).

Geschwind (1987) has hypothesized that the basic genetically determined pattern of the human brain is one with strong left hemisphere asymmetry, perhaps evolved for support of human language and handedness. If such asymmetry is already apparent in early human fetal development, then any influences that delayed left hemisphere growth would tend to produce a brain that was more symmetrical.

It has become clear that, among other factors, both levels of gonadal steroids and

adrenocortical steroids affect the asymmetric pattern of the cerebral cortex. As Lewis and Diamond (1995) report, several behaviors seen in rats, especially male-typical sexual behaviors, some forms of aggression, and some skills related to maze-learning, are related to the presence of estrogen in the male brain at specific, critical periods during gestation of the male fetus. The source of the estrogen is conversion of fetal testosterone into estrogen by an aromatizing enzyme found in neural tissues. Testosterone depletion, inhibition of conversion of testosterone to estrogen, and blockage of estrogen receptors all result in more female-typical behavior and less male-typical behavior in rats. Behavioral changes of such a nature are found to be highly correlated with steroid-dependent anatomic and morphological changes in specific nuclei of the hypothalamus. In addition, they also appear to be correlated to changes in the cerebral cortex, such that similar steroid-dependent patterns of growth are seen in the cerebral cortex and are related to the development of cerebral cortical asymmetry (Lewis and Diamond, 1995).

For example, the right cerebral cortex of male Long-Evans rats is significantly thicker than the left; in females the cortex is more symmetric. If asymmetry is observed in females, the left side tends to be thicker than the right (Diamond et al., 1975). The action of sex hormones in determining this asymmetry was demonstrated by removing the gonads (Diamond, 1984). In the Long-Evans rat, the left-right and male-female differences are related to the asymmetric distribution of estrogen receptors in the cortex (Lewis and Diamond, 1995; Diamond, 1993).

Several pieces of information are now available that allow a preliminary attempt at assessing the underlying causes of cerebral asymmetry in terms of sexual dimorphism (Lewis and Diamond, 1995). It is clear that cortical asymmetry is altered by both prenatal and early postnatal manipulation of sexual steroid levels. It is also clear that there are sex differences in the level of serum testosterone during developmental differentiation of the cerebral cortex. *Manipulation of testosterone levels at this time alters cortical asymmetry.* The actual mechanism is

complex. There is experimental evidence that testosterone acts on the developing cerebral cortex primarily by conversion to estrogen and subsequent interactions with estrogen receptors; however, because of the existence of alpha-fetoprotein in the fetal brain in large quantities (enough to bind all circulating estradiol and estrone), generation of estrogen by cortical aromatization has not been demonstrated neonatally. Although the potential exists for the effects of testosterone to be mediated by cerebral androgen receptors, which are also present in the prenatal brain, clear evidence of such effects in humans remains undemonstrated. Since, in rats, cortical asymmetry is present at birth and androgen receptors are undetectable prenatally, it appears that any mediating effect occurs relatively late. Although general aromatase activity has not been detected in the neocerebral cortex of rats, it has been reported in hamsters. It has also been observed in fetal rhesus macaques, with aromatase activity found present in the frontal cortex at higher levels than found in adults, and with greater activity in fetal males. In addition, the administration of 1,4,6-androstatriene-3,17-dione (ATD), an inhibitor of aromatase, can cause alterations in normal cortical growth patterns. This tends to provide at least indirect evidence for an aromatization effect on cerebral cortical differentiation in specific areas of the cortex, especially during gestation.

Thus, at least in rats, cerebral cortical asymmetry appears to be largely hormone-dependent, testosterone seems to be responsible for the sexual dimorphism in cortical asymmetry, and aromatization to estrogen and interaction with cortical estrogen receptors seems to be the way testosterone causes the sex differences in cortical asymmetry (Lewis and Diamond, 1995).

Information on the effect of fetal testosterone on the development of the fetal brain is also available from studies of primates. For example, Michael et al. (1989) have demonstrated that testosterone secreted by the fetus in rhesus macaques around 120 days of gestation can influence the brain's subsequent development. Their results suggested that aromatization and, then, estrogen receptors influence the effects of testosterone

on at least the hypothalamus and amygdala of the fetus.

As in rats and nonhuman primates, so also in humans. The presence or absence of specific sex hormones during critical stages of human prenatal development plays a role in the sexual differentiation of the developing brain (Halpern, 1992). The first fully developed neurons begin to form a rudimentary brain at about 7 weeks after conception, which, coincidentally, is also about the time that the fetal testes begin secreting testosterone. The connections between neurons form at about 28 weeks after conception, and these connections between neurons are necessary for the establishment of the higher level cognitive activities that define the human mind (Halpern, 1992).

It is clear that sex hormones not only influence the development of the brain itself in terms of gender differences, but that these sex hormones continue to have a direct influence on male/female differences throughout life. For example, studies have demonstrated that cognitive patterns fluctuate with variations in sexual steroid levels in both adult males and adult females, regardless of the cause of the varying levels (Kimura and Hampson, 1994; Chowen et al., 1993). Additionally, it is clear that testosterone influences spatial cognition in older men; an increase in testosterone results in significant enhancement of spatial cognition, but not in other cognitive domains (Janowsky et al., 1994). Testosterone supplementation influences the endogenous production of estradiol which, in turn, has been shown to have an inverse relationship with spatial cognitive performance. This effect of testosterone seems to be through its influence on estrogen (Janowsky et al., 1994).

The establishment of hormone-sensitive fluctuations in cognitive abilities combined with information about early organizational effects of sex steroids on the human brain suggests that sexual dimorphism in cognitive abilities is a product of both current hormone levels and of the early hormonal environment (Kimura and Hampson, 1994).

The effects of sexual steroids on behavior have been demonstrated indirectly by studying the effects of fetal testosterone produc-

tion on the behavior of their mothers during pregnancy. Studying female Mongolian gerbils, Clark et al. (1993) demonstrated a correlation between number of male pups fetally and maternal plasma testosterone levels. They interpret the results of their study as demonstrating that fetal males excrete quantities of fetal testosterone that are biologically significant—the significance of which is evidenced by masculinizing the behavior of their mothers late in pregnancy. Studies of mammals closer to humans do not necessarily corroborate this finding. For example, Nieuwenhuijsen et al. (1988), studying pregnant stump-tail macaques, were unable to demonstrate an effect of fetal gender on the aggressive behavior of pregnant mothers, although they did note a general decline in aggressive behavior across the board among the pregnant stump-tail macaques. However, it should be noted that determining the effect of fetal testosterone alone on their mothers' aggression might not provide the resolution needed to resolve behavioral differences in general related to lateralization. Other researchers have shown that androgen receptors are present in the brains of fetal rhesus macaques during the critical period for sexual differentiation (Handa et al., 1988), which implies a potential role in lateralization of behaviors, if not in the structures of the brain itself. Additionally, in humans, the amount (and severity) of nausea and vomiting in pregnancy should be related to fluctuations in levels of circulating sexual steroids in the maternal system, with subsequent consequences related to maternal well-being and fetal outcome.

Obviously, many factors are involved when speaking of influencing the final dimensions of the cerebral cortex, including both ones related to general metabolism and ones related to all the changing levels of other hormones related more directly to growth. Even so, it may turn out that estrogen is substantially responsible for differentiation of the cerebral hemispheres producing sexually dimorphic asymmetries. The many parts of such asymmetries may well occur before the maximum periods of fetal growth and consolidation of structures (Lewis and Diamond, 1995).

As Lewis and Diamond (1995:42–43) state:

One perspective that may help us to understand these complex hormonal systems for sexual differentiation is that every organism requires multiple levels of control over maleness and femaleness. Consider the number of regions in which sex differences exist, each with its own developmental timetable and its own interactions with neighboring and distant tissues. In the central nervous system alone, the differentiation of sexual behaviors involves sexual dimorphism of the hypothalamus, preoptic area, amygdala, pituitary, spinal cord nuclei associated with pelvic musculature, perhaps the cortex, perhaps the hippocampus, perhaps the pineal body; sexual differences in exploratory behavior may involve cerebral cortex, striatum, and hippocampus; sex differences in paternal and maternal behavior involve the hypothalamus, pituitary, and probably additional brain regions as well; sex differences in perception involve differential organization of a variety of sensory processing pathways and associative connections.

Although the probability of modifying the levels of a single hormone during fetal and postnatal development to produce all these products of sexual dimorphism may seem to be extremely remote, much of the human male/female differences in hemispheric asymmetry can be explained by relatively small changes in levels of circulating sexual steroids during early fetal development. We believe that the bulk of the available evidence supports Geschwind's (1987) hypothesis regarding the effect of testosterone on fetal brain growth, such that growth retardation will generally be more marked in certain left hemisphere regions in males, "who will therefore show on the average a greater degree of shift to right-hemisphere participation in handedness and language and will therefore more likely have augmented right hemisphere skills. In addition, they may have elevated skills related to unaffected regions in the left" (Geschwind, 1987:12). If correct, the final effect on the amount of asymmetry would be determined mainly by the amount of *usable* fetal testosterone and the timing of hemispheric growth.

ARCHAEOLOGICAL EVIDENCE FOR THE EVOLUTION OF HUMAN SPATIAL ABILITIES

Evolutionary science employs three major methodologies: study of fossils, comparative

anatomy and behavior, and comparison to human ontogeny. None is particularly helpful in a study of the evolution of human spatial abilities. Fossils, even endocasts of brains, tell us little or nothing about spatial ability. Comparative evidence can inform us about ape abilities, and by extension the probable abilities of our common ancestor, but are uninformative about specific developments after the phylogenetic split. Ontogeny can reveal the development of spatial abilities in individual humans, and can provide hypotheses for developmental sequences (e.g., Parker and Gibson, 1990), but can reveal nothing about the timing or context of evolutionary developments. Luckily, in the case of later hominid⁵ evolution at least, we have a sequence of hominid products in the guise of stone tools. The production of these tools required their makers to organize action in space and this gives us a narrow window through which we can assess spatial abilities.

Most stone tools are produced by fracturing stone; this produces a sharp edge that is useful for numerous specific tasks. The techniques by which stone can be fractured ("knapped") vary in the degree of skill required, at least as measured by the amount of time and practice required to learn a particular technique. Some knapping techniques that appeared very late in human prehistory require years of practice to perfect; however, most are not so complex. The simplest tools are produced by using a hammer (usually another stone) to break a piece (flake) off of a larger mass of rock (core) (Fig. 5). More complex tools involve flaking a core several times, and it is the organization of this action of flaking that requires spatial concepts of varying sophistication (Wynn, 1989; Robson Brown, 1993). By examining the patterns of flaking on artifacts manufactured at varying points in human evolution, it is possible to document an evolutionary sequence of spatial abilities. There is, unfortunately, a rather serious methodological caveat to this approach. How do we know that

hominids used their most sophisticated spatial thinking in the manufacture of stone tools? It is impossible logically to eliminate the possibility that hominids at any point in the prehistory used more sophisticated spatial thinking in behavioral domains that are archaeologically invisible. Nevertheless, we have little option but to consider the archaeological record as more or less reliable.

Relatively little work has been done on the cognitive basis of stone knapping. Previous work of one of us (T.W.) applied the developmental theory of Jean Piaget to the record of stone artifacts (e.g., Wynn, 1989). Piaget's work was appropriate because he and Barbel Inhelder made extensive studies of the ontogeny of spatial ability (Piaget and Inhelder, 1967). More recently, Robson Brown (1993) examined stone artifacts from a rather different cognitive perspective, one that emphasizes a modular theory of cognition rather than the unified theory advocated by a narrow Piagetian approach. She employed the concepts of mental rotation, element recognition, oblique angles, and visual attention. These specific spatial abilities are more amenable to the literature on cognitive sex differences than the geometric concepts used in the Piagetian approach to spatial ability (order, symmetry, parallels, and so on), and we will rely on them extensively in our analysis. Recent work by Pelegrin (e.g., 1990), and his students and associates, has developed a powerful method ("chaîne opératoire") for describing sequences of action in stone knapping. Thus far, the results of this approach have been primarily descriptive, but it holds great promise as a basis from which cognitive assessments could be made (see also Schlanger, 1990).

To date, archaeological studies of spatial cognition have been few and tentative, but they have produced results that document some of the evolutionary developments in spatial thinking. Unfortunately, identification of sex differences in the abilities of prehistoric people may well be beyond our reach; we simply do not know the sex of our prehistoric stone knappers. For the very recent past, it is possible to make judicious assessments of gender roles, but these assessments are based heavily on analogy to

⁵We are using the definition of hominid that includes only humans and human ancestors, as opposed to the more recent trend to include all african apes in this taxon.

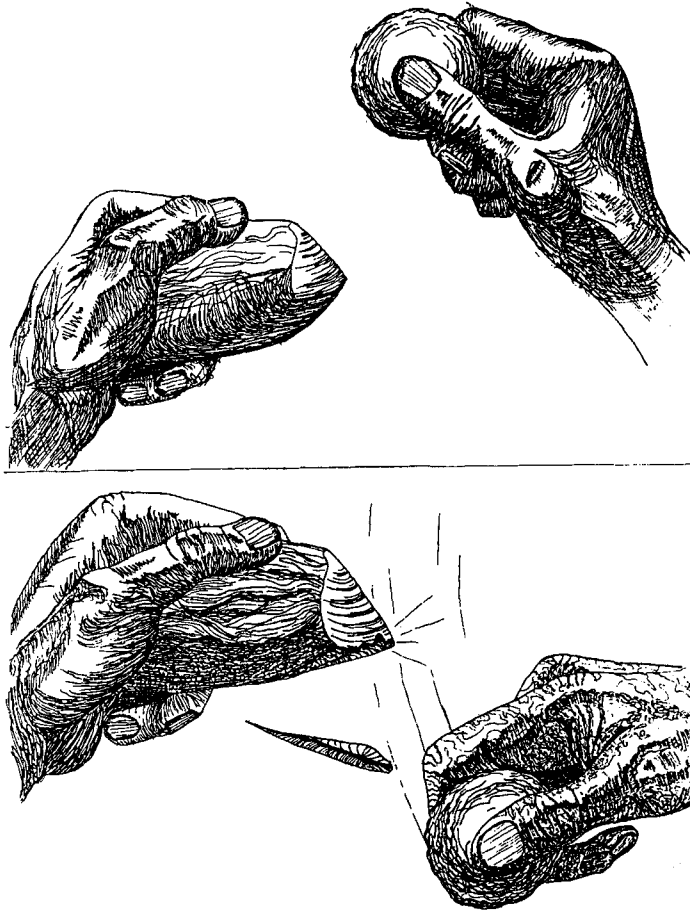


Fig. 5. The basic action of stone knapping.

modern humans. In fact, they are most convincing when archaeologists can trace a direct historical link between their archaeological remains and a known historic or modern group. At best this yields a time depth of a few thousand years. For most of human evolution we do not know which sex did what. Nevertheless, we can take the cognitive spatial abilities for which there are reliable sex differences in the modern world and try to document the evolution of each. This may provide insight into the evolutionary timing and context of the specific abilities, which in turn should bear on the hypotheses summarized earlier.

THE EARLIEST STONE TOOLS

The earliest flaked stone tools so far discovered were manufactured about 2.5 million years ago in what is today Ethiopia (Harris, 1983). They consist of simple stone flakes and the cores from which they were removed. It is likely that the hominids set out to produce the flakes, which are very sharp (Toth, 1985b; Isaac, 1984). However, to produce the flakes the knappers had to organize their action *on the core*, and this controlled knapping produced a pattern of flake "scars" that reveals something of their spatial understanding (Fig. 6). The hominids

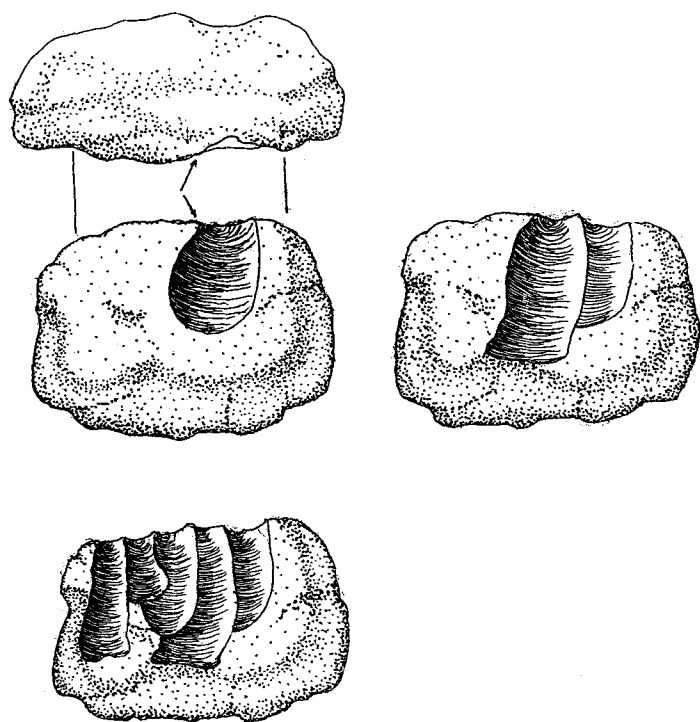


Fig. 6. The arrangement of successive blows on a core produces patterns of flake scars, from which it is possible to reconstruct sequences of action and make assessments of spatial concepts.

clearly did not strike the cores in a haphazard manner, but directed the blows toward particular positions on the core that were most likely to produce a flake of reasonable size. This required several abilities. At a minimum the knapper had to be able to recognize acute angles at the edges of the core; oblique angles cannot be flaked (Toth et al., 1993) (Fig. 7). Also, the knappers placed blows at the margins of negative scars made by previous flake removals (which, not surprisingly, often present an acute angle). Often, the knapper maintained an acute angle by flaking along a particular plane of the core, occasionally by alternating back and forth on either side of the plane ("bifacial" trimming or flaking). By 2 million years ago we also find flakes that were further modified by trimming along edges, sometimes resulting in a projection or "awl" (Fig. 8).

The spatial abilities necessary for this kind of knapping are not very sophisticated. We need not posit frame independence, or mental rotation, or spatial visualization. In-

deed, the knappers need only have attended to the relatively simple topological relationships of proximity and boundary, and possibly order (placing blows in sequence along an edge). The one possible nontopological concept was the idea of a projection, which requires some discrimination of pointed vs. smooth. Piaget and Inhelder identified all of these in the spatial repertoire of young children (in Piaget's preoperational stage). Interestingly, children at this age are too young to be tested for the spatial concepts typically cited in the sex difference literature, so we do not know if these simple spatial abilities also have a sex difference.

The evolutionary implications of this assessment of the earliest stone knappers are controversial. W. C. McGrew and one of us (T.W.) have argued that the spatial repertoire of these stone knappers differed little, if at all, from that used by modern apes (Wynn and McGrew, 1989). When modern apes are given Piagetian type tasks, they generally perform at a preoperational level

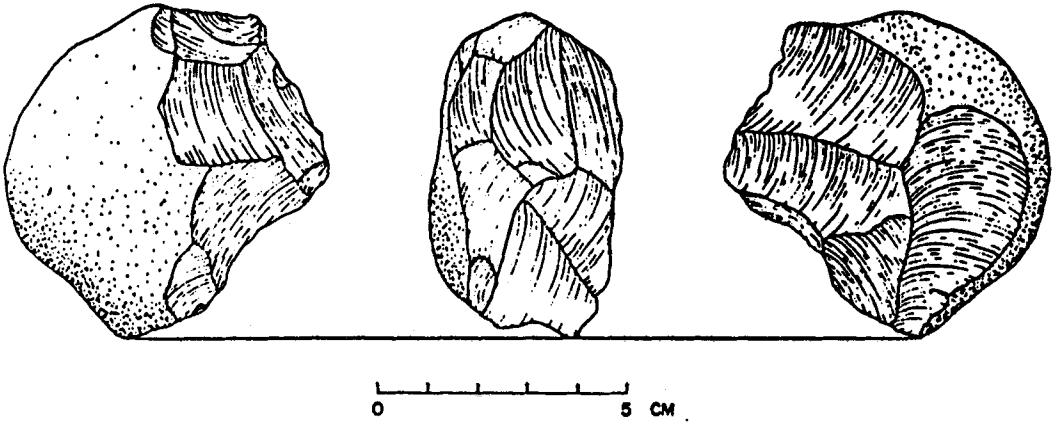


Fig. 7. A "chopper" from Olduvai Gorge (about 1.7 million years old). This artifact did not require the kind of spatial concepts for which there is a sex difference in modern humans.

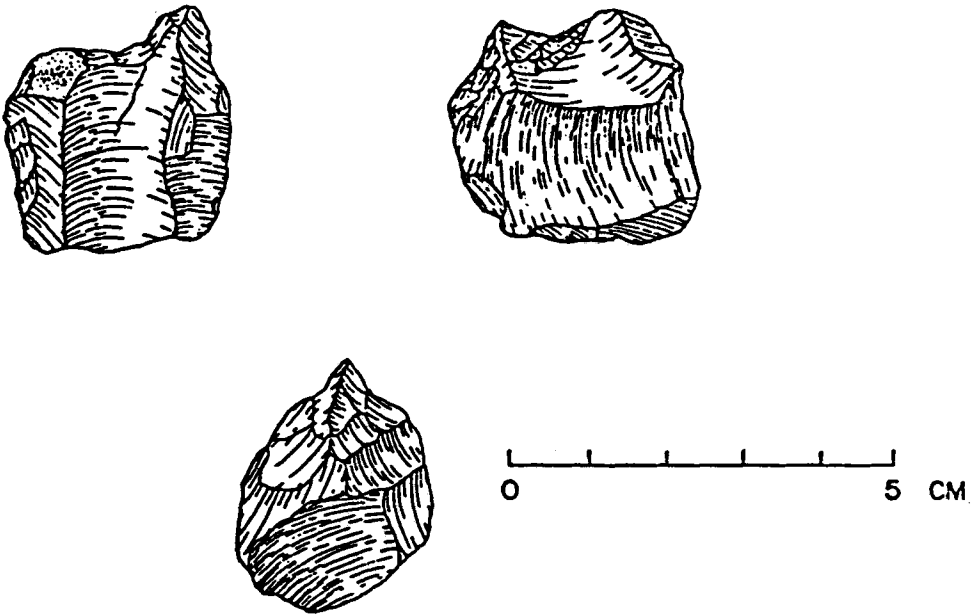


Fig. 8. "Awls" from Olduvai Gorge.

(see Parker and Gibson, 1990, for a recent compilation of this literature). This is also true for specifically spatial abilities, though comparatively few controlled tests have been done. Chimpanzees in captivity have occasionally been given opportunities to draw and paint. In the one controlled experiment of chimpanzee drawing (Boysen et al., 1987),

the subjects did not mark randomly, but paid particular attention to the boundaries of the paper, and to the boundaries of predrawn squares. In natural contexts, they use the same kinds of simple topological concepts that we can reconstruct for the earliest stone tool makers: proximity in smashing nuts with hammers, boundaries (especially in-

side-outside) in extracting termites from mounds, and possibly in the weaving of branches necessary for a sleeping platform (Wynn and McGrew, 1989).

Recent experimental work with a bonobo (pygmy chimpanzee) provides some corroboration for the apelike abilities of early tool makers, but also point to certain more "advanced" abilities possessed by the early hominids. Nick Toth and Sue Savage-Rumbaugh have taught the bonobo Kanzi to flake cores and use the flakes to cut ropes securing boxes (Toth et al., 1993). However, Toth argues that Kanzi's ability, while impressive, does not match that of the early hominid tool makers. In particular, Kanzi does not appear able to control the knapping blows as precisely as those we see on the early tools. This may be a problem in motor control (knapping requires considerable strength with simultaneous fine motor control), but Toth believes that the problem is also cognitive. Kanzi does not recognize the best flaking angle on the edges of cores, but proceeds more haphazardly. Toth argues that Kanzi does not have a complete understanding of the knapping procedure and that therefore the early hominids were cognitively advanced compared to modern apes. What does appear clear from Toth's work with Kanzi is that apes cannot duplicate the accomplishments of early hominid stone knappers. By 2.5 million years ago evolution had produced a creature that possessed an ability not possessed by other apes, and one component of this may have been an ability to discriminate angles (this is corroborated, weakly, by the presence of awls in some early assemblages).

It is important not to overemphasize this development in spatial ability. For one thing, Kanzi's poor performance may be the result of motor coordination differences; that is, Kanzi may see the angles but just not be able to deliver the blows precisely enough. More important, however, we still do not see in the early tools, or in Kanzi's products for that matter, evidence for some of the more abstract spatial abilities within which cognitive sex differences appear. We see no use of external spatial frames (and hence no problems in frame-related spatial perception), and no mental rotation or obvious

use of complex spatial visualization. Even if they were slightly more sophisticated than that of a chimpanzee, the spatial abilities of the earliest tool makers were still very primitive.

Based on this archaeological evidence, we feel it is reasonable to conclude that the sex difference we see in modern humans was *not* in place during the first million years of stone knapping. Since the abilities in question seem not to have been employed at all, it seems unlikely that there was a sex difference. After 1.4 million years ago the picture becomes more complex, and it is best to consider the archaeological record for each of the spatial abilities separately.

SPATIAL PERCEPTION

The first evidence for a material culture that was significantly different from that documented for apes is provided by the first bifaces, which appeared in East Africa about 1.4 million years ago (Wynn, 1993; Wynn and McGrew, 1989). These early bifaces were the first tools with an obvious overall shape. Before this, stone knappers had only attended to the shape of edges, the size of tools, and in some cases the pattern of flakes relative to one another (Toth, 1985b). The early hand-axes have a more or less "tear drop" shape in outline, with a pointed "tip" and an unpointed, rounded "butt" (Fig. 9). The knappers produced this result by trimming the margins of a core bifacially. Sometimes they trimmed the entire margin of the tool, but often they left segments of the margin untrimmed, most commonly the butt. The "blanks" on which knappers produced bifaces were, in fact, often very large flakes that had been removed from small boulders by a special two-handed hammering technique (Jones, 1981). In this sense the manufacture of a biface incorporated two distinct steps in manufacture: production of a large flake and modification into a biface.

In manufacturing a biface, the knapper needed to use a spatial frame of reference that was independent of the core shape itself. For these early bifaces this was a simple bilateral symmetry; one side of the artifact mirrored the other. This is not the fine congruent, bilateral symmetry we encounter so

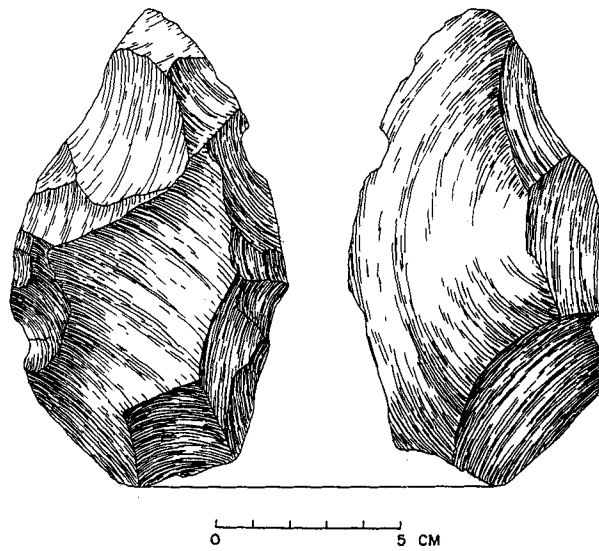


Fig. 9. Biface from the 1.4-million-year-old site of West Natron. This artifact required a rudimentary notion of symmetry.

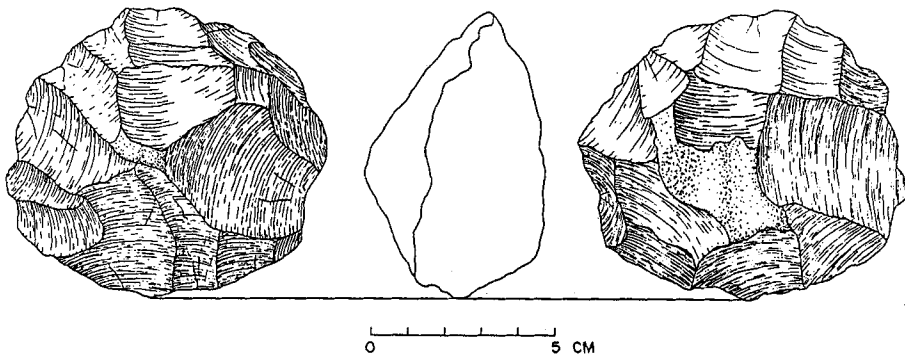


Fig. 10. A "discoid" from Upper Bed II at Olduvai, about 1.2 million years old. This artifact required a rudimentary notion of diameter or radius, which is a spatial quantity.

often in modern cultural products. Rather, it is a mirroring that reverses only qualitative characteristics of a shape: a recurve (S-shape) or a shoulder, for example. The knappers made no attempt to produce a quantitative duplicate on the mirrored side. Even such simple mirroring requires imposition of a spatial framework on the perceptual field of the artifact. If the knapper wanted to produce even a simple bilateral symmetry, he or she had to be able to ignore the configu-

ration supplied by the naturally occurring outline. We do not see such frame independence in the products of apes.

In a few instances, these early biface makers appear to have imposed one kind of simple quantitative framework. The resulting artifacts are termed discoids (Fig. 10). The knapper appears to have set out to regularize the diameter of the artifact, and a diameter is a quantity of space. True, this quantity is very local, and also available to direct per-

ception, but, like bilateral symmetry, it requires that the knapper ignore the natural configuration or frame and follow the guidelines of a different framework. The concepts of diameter and symmetry indicate that the knappers' spatial understandings were not dictated by the local spatial frame of a cobble or large flake, but existed as concepts held in the mind independent of a particular task. This is a matter of visual perception, and is one of the abilities that shows a significant sex difference in modern humans.

The complexity of spatial frames increased significantly over the course of the 1 million plus years that stone knappers made bifaces. By 300,000 years ago, the symmetry of bifaces had become a true euclidean symmetry in which a congruent shape is mirrored (Fig. 11). Congruency requires both qualitative and quantitative equivalency; some notion of spatial size must be employed. Such a euclidean symmetry is a sophisticated, external spatial framework that must be imposed on an artifact. It is not a natural feature of stone (at least not in the cryptocrystalline stone used in stone knapping). This is, moreover, a much more abstract kind of spatial frame than that employed by the first biface makers. It was also conceived of and executed in three dimensions, rather than two, but this latter feature taps another spatial ability—mental rotation.

In sum, the record of early stone tools documents an evolutionary sequence of abilities in spatial perception. By the time of early *Homo erectus* stone knappers were able to employ independent frames of reference, and by the time of early *Homo sapiens* the artifacts indicate a sophisticated ability in frame independence. If there was selection for this ability, it was either continuous over the course of *Homo erectus*' tenure, or it occurred early, and then once again late. However, it is not clear what selective advantage this ability would provide for hunting, or foraging, or male access to mates. Indeed, its only obvious application was in making more regular tools, a feature which bears little or no relevance even to a tool's mechanical function.

MENTAL ROTATION

As we discussed earlier, mental rotation is the ability to manipulate images of objects

in the mind; to unfold boxes or rotate complex three-dimensional shapes. There is some evidence that simpler feats of mental rotation can be performed by nonhuman primates (Georgopoulos et al., 1989; Vauclair et al., 1993). In the most impressive example, Jacques Vauclair and colleagues had baboons identify rotated versions of two-dimensional figures (a capital F, for example). That a nonhuman primate can perform some tasks of spatial rotation underlines some of the difficulties that arise in developing evolutionary scenarios for cognitive abilities. Is mental rotation a single cognitive ability, or does it incorporate several different abilities? If it is a single ability, then Vauclair et al.'s work suggests it is an old cognitive adaptation possessed by many anthropoids, in which case it would be very interesting to know if there is a sex difference in nonhuman performance. On the other hand, the tests employed in the human sex difference literature use three-dimensional figures. Are mental rotations of three-dimensional figures more difficult than rotations of two-dimensional figures? Is dimensionality a separate cognitive ability?⁶ Until comparative psychologists demonstrate that nonhuman primates can perform complex tasks of three-dimensional rotation, we must assume that this is not a pan-primate ability, and that it evolved at some point in the hominid line.

Robson Brown (1993) has recognized mental rotation in the stone tools from Zhoukoudian (about 500,000 years ago), but a more amenable subject is once again the biface. The earliest bifaces required no ability to rotate images (Wynn, 1989). The stone knappers modified cores and large flakes into shapes, including symmetry and diameter, that they could see directly; the model was always available to perception. We need not posit that these early biface makers con-

⁶More troubling than mental rotation in the Vauclair experiment was speed of performance. Baboons selected the correct image ten times faster than humans. "For every 60° rotation, the average increment in response time was 207ms for the humans, but 18ms for the baboons" (Vauclair et al. 1993:101-102). This suggests to us that the baboons were using other cues in the selection of correct figures, while the humans were actually rotating the images.

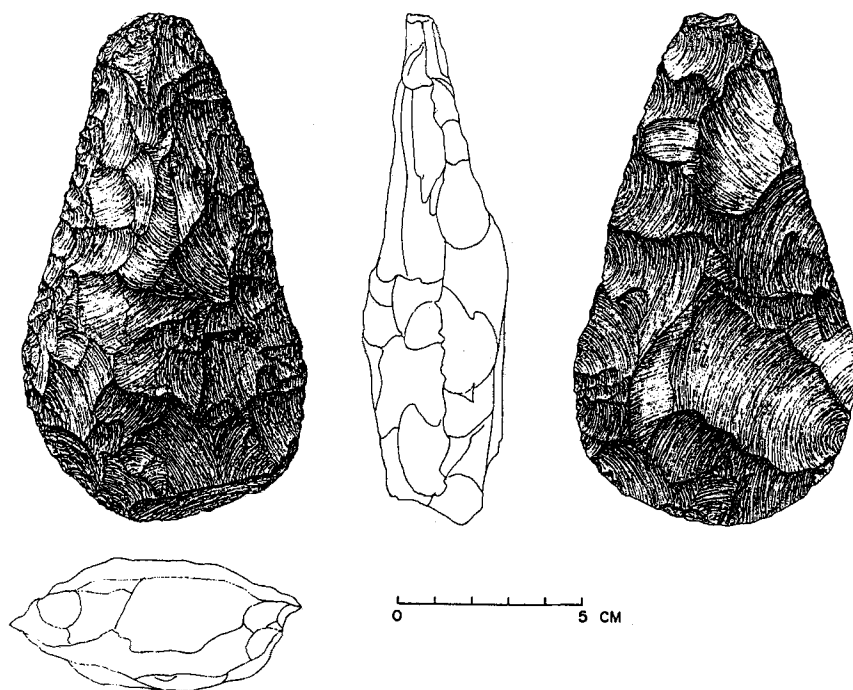


Fig. 11. An unprovenienced biface from Europe demonstrating congruent symmetry in three dimensions.

ceived of an image that they then rotated in their minds. However, there is reason to believe that these stone knappers were able to construct alternative perspectives to some degree. The ability to “see what another sees” is an important component to observational learning (Whiten and Byrne, 1991; Tomasello et al., 1993). Early bifaces are a standardized pattern that many, if not all, stone knappers learned to produce. The only way to learn such a shared concept is by constructing what another sees (Mithen, 1994), and understands to be appropriate (language would be a help, but would not be sufficient [Wynn, 1991]). The ability to imagine what another sees is almost certainly possessed by chimpanzees (Whiten and Ham, 1992), but there is considerable disagreement in the primate literature about how much a chimpanzee can conceive of what another understands. The ability to imagine what another individual understands to be appropriate is an ability that has not (yet?) been documented for chim-

panzees, and therefore appears to distinguish early biface makers from apes and earlier hominids (Wynn, 1993). Even this ability, however, is not equivalent to mental rotation, in which an image constructed by the mind is manipulated and transformed.

By 300,000 years ago, and perhaps before, stone knappers could produce artifacts with congruent symmetry in three dimensions. Many of the bifaces produced at this time have regular symmetrical cross-sections. If one were to cut through the biface in Figure 11 at any angle, the resulting cross-section would be symmetrical. Unlike the cross-sections of cylinders, parallelepipeds, and other regular three-dimensional solids, the cross-sections of a biface are not necessarily symmetrical if the profile is symmetrical, so the knappers could not have achieved the desired result by simply checking the profile or end views. The unobservable cross-sections must, therefore, have been mental

constructs. The knapper had to visualize—to imagine—the cross-sections and assess the effect that trimming would have on these invisible but visualized patterns.⁷ This is the same cognitive skill that is used in tests of mental rotation; the ability to manipulate an image in the mind and come to an understanding of how it appears from an imagined perspective.

The archaeological record indicates that mental rotation, in the narrow sense of being able to rotate an image of a three-dimensional object, appeared late in human evolution, probably about the time of the transition from *Homo erectus* to Archaic *Homo sapiens*. While it does appear that early *Homo erectus* was better at constructing alternative points of view than its predecessors, the narrow skill of mental rotation is not evident that early. This conclusion has obvious implications for the evolution of sex differences. Mental rotation in the narrow sense demonstrates the most salient sex difference in all of cognition. If natural selection produced this difference, then we must identify a selective factor that emerged relatively late in human evolution.

SPATIAL VISUALIZATION

While not as clear as the evidence for spatial perception and mental rotation, the archaeological record documents a possible sequence of increasingly complex achievements in spatial visualization. In stone knapping, this would be a matter of visualizing a final artifact “imbedded” in a core or flake blank. Unfortunately, it is unclear to what degree, if any, stone knapping requires such visualization of imbedded figures. The vast majority of stone artifacts result from applying a procedure to a core of appropriate size (Dibble, 1987). In these cases there is no need to “see” the artifact in the blank. Even with artifacts, like bifaces, whose shape was clearly intended, it may not

have been necessary to visualize a specific pattern in the complex background of the core. Nevertheless, the archaeological record documents some abilities that are perhaps related to spatial visualization.

It is possible that effective stone knapping requires an ability to detect edge angles that are most conducive to removing large flakes. If true, this may indicate that even the earliest stone knappers had a spatial visualizing ability not possessed by modern apes, who apparently cannot find appropriate angles, even though they can remove small flakes from cores (Wright, 1972; Toth et al., 1993, see above). But even the earliest stone knappers attended only to the configuration of edges, and did not consider the overall shape of the artifact, so the visualized target, if there was one, was very simple. With the advent of the biface, the visualized pattern takes a step up in complexity (see earlier discussions), the knapper having to consider the shape of the whole artifact, in addition to the configuration of the edge. But even here, it appears unnecessary to visualize a specific pattern ahead of time.

Contemporary with the appearance of the fine later Acheulean bifaces was the appearance of a technique of flake manufacture termed “prepared core” technique. Here the knapper prepared a mass of stone into a core in such a way that the shape of the core “predetermined” the size and shape of a single large, thin flake. Occasionally, these large flakes were further modified into bifaces or other types of tools. Archaeologists have often pointed to the necessity to “see” the ultimate flake in the core. If true, then this would represent a sophisticated ability to visualize a pattern in a confusing background, much like the visualization in an embedded figures test. However, once again this may be an overinterpretation; the shape may follow from the procedure, not a visualized pattern (Fig. 12).

The archaeological evidence for spatial visualization is not as clear as the evidence for mental rotation or even spatial perception. What little evidence there is also points to a late evolution, roughly contemporary with mental rotation. Spatial visualization, especially as represented by the embedded figures test, is the one spatial ability that has

⁷Most research on the cognitive basis of knapping has focused on sequential procedures and chains of decision making, and much of this has been based on self reporting by knappers. Self reporting is a notoriously misleading source of understanding. We have only a self report from a stone knapper (Charles Keller) to corroborate our interpretation of the difficulties that arise in producing regular cross-sections.

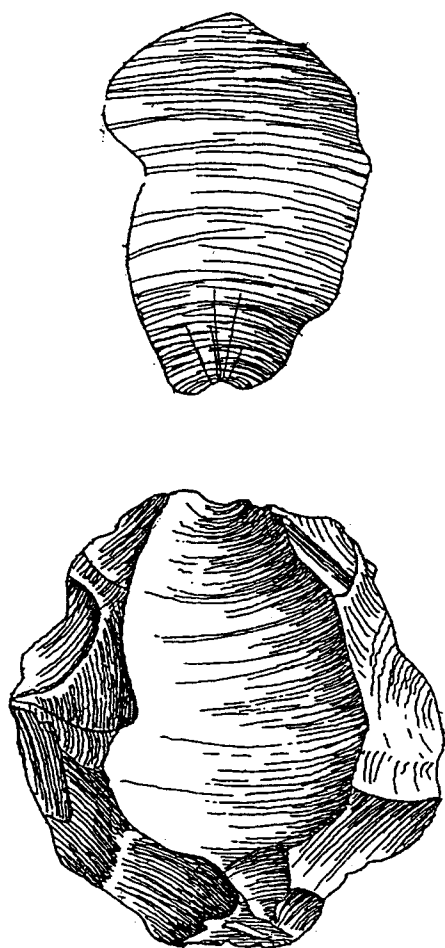


Fig. 12. A Levallois core and flake.

shown a female advantage. If Eals and Silverman (1994) are correct in attributing selection for this ability to female foraging in environments with complex backgrounds, then this ability must have appeared late in human evolution. However, the archaeological record suggests that such foraging has always been a part of the hominid adaptation, as it is for living apes. Eal's and Silverman's hypothesis therefore appears an unlikely one.

SPATIOTEMPORAL ABILITY

Next to mental rotation, spatiotemporal ability demonstrates the largest sex differences in the experimental literature. Unfor-

tunately, of the four spatial abilities addressed in this paper, it is also the most difficult to document in the archaeological record; time is a component of spatiotemporal thinking and the archaeological record just does not preserve time on this scale. This places any archaeological interpretation in the uncomfortable position of trying to document material correlates of finely timed actions. The only real candidate for this is the projectile, but even this would not itself be enough. In order to document evolution in spatiotemporal ability it is also necessary to show that accuracy has improved over time. Clearly, archaeologists cannot document accuracy *per se*, but we can estimate the relative investment in projectile production. Arguably, the more accurately one can throw, the more one would be willing to invest effort in individual projectiles.

Aimed throwing in general appears to be a hominid activity, but its antecedents almost certainly lie in the agonistic throwing documented for many nonhuman primates. Most anthropoid primates throw objects in agonistic situations, but in general the accuracy of this throwing is poor (though unaimed throwing does occasionally connect with a target, as many primatologists can attest). Modern humans do aim their projectiles, however, and can achieve high degrees of accuracy. Just how this ability evolved is the question at issue.

The hominids who made the first stone tools either did not use projectiles or did not invest any effort in producing them. Most of the early archaeological localities in East Africa have yielded unmodified cobbles that had been carried to the sites, and some archaeologists have speculated that these were used as projectiles to frighten off predators. There are, however, other interpretations, including arguments for raw material caching (Potts, 1988). In addition, there are modified cobbles known as spheroids, which have also been cited as possible projectiles, but Toth (1985b) has convincingly demonstrated that the spheroid shape resulted from repeated use as a bashing tool. In sum, there is no reason (e.g., the projectiles themselves or remains of animals that clearly had been hunted) to conclude that the earliest stone knappers used aimed throwing (contra Par-

ker and Gibson, 1979). If they did throw objects, they were probably no more accurate than modern chimpanzees.

O'Brien (1981) has suggested that bifaces were projectiles, and Calvin (1993) has taken this a step further to suggest that aimed throwing was the most important selective factor in the evolution of human cognition. Their arguments are based on experiment (when thrown handaxes tend to land tip down) and geologic context (handaxes are often found in stream and spring deposits, i.e. where animals would come to drink). However, most archaeologists reject the handaxe-as-projectile argument. Other experimental applications (Schick and Toth, 1993) and edge damage analyses (Keeley, 1980) indicate that handaxes were multiple purpose tools, useful in butchery and plant processing. More to the point, the kind of discus-style throwing posited by O'Brien seems unlikely to have selected for spatiotemporal thinking.

Spears made an appearance about 300,000 years ago at the English site of Clacton-on-Sea. This famous example is a simple yew shaft sharpened by a stone tool (Oakley et al., 1977). While potentially an effective thrusting and penetrating weapon, it need not have been thrown. If we assume that it was thrown, then this spear marks the first known projectile in which hominids invested significant effort; if it was thrown it was certainly aimed. Such a find is extremely rare in palaeolithic archaeology, and most arguments concerning projectiles are based on stone points. Wymer has argued for the presence of stone points in Middle Stone Age (ca. 100,000) contexts in South Africa (Singer and Wymer, 1982), and Shea (1993) and Kuhn (1993) have argued for hafted points in Middle Palaeolithic contexts in Israel and Italy respectively. Again, if these were thrown projectiles, then the greater investment of effort suggests greater confidence in accuracy. The most dramatic development in projectile technology is associated with the Early Upper Palaeolithic in Europe (40,000 years ago or so). Bone and antler projectile points, along with antler spear throwers, indicate a considerable investment in missile and launch technology, and by extension a greater confidence in the accuracy of throwing itself.

There are too many unknowns in this summary to make reliable assessments of spatio-temporal cognition. About all that we can conclude with confidence is that evidence for aimed throwing is relatively late in human evolution (after 300,000) and heavy investment in throwing is *very* late (after 40,000). The use of spear throwers during the Upper Palaeolithic would almost certainly have required the abilities measured in tests of spatiotemporal ability. Any selection for spatiotemporal ability by means of aimed throwing in hunting could only have been very late in human evolution, later even than selection for mental rotation.

OTHER POSSIBLE ARCHAEOLOGICAL CORRELATES

Most of the hypotheses for the evolution of the sex differences in spatial cognition have focused on foraging and/or ranging. Both are visible to some degree in the archaeological record, and it is therefore possible to match what we know about the evolution of spatial thinking with what archaeologists know about the evolution of foraging and ranging.

The only time in hominid evolution when there was a clear coincidence of development in spatial thinking, foraging, and ranging was with the advent of *Homo erectus*. The archaeological remains of *Homo erectus* differ in number of significant ways from that of earlier hominids. As we discussed earlier, there was a clear difference in the spatial concepts used in stone tool manufacture. There was also a marked difference in the locations of *Homo erectus* sites, both in terms of geographic distribution and the physiographic locations of activity. *Homo erectus* lived in a much wider range of habitats than earlier hominids, including hotter and drier, and higher and cooler environmental zones. There is evidence that much of *Homo erectus*' activity took place well away from the woodland and riparian habitats favored by earlier hominids (Cachel and Harris, 1995). Indeed, an essential element of *Homo erectus*' niche appears to have been an adaptation to hotter, drier, open savannas (Walker and Leakey, 1993). Somewhat paradoxically, we know less about the foraging patterns of *Homo erectus* than that of earlier hominids, largely because the sites are in poorer geo-

logic context. However, the change in distribution and niche indicate that hominid foraging had probably changed. There is some evidence that meat played a more important part in the diet (Cachel and Harris, 1995), but it is entirely unclear to what extent, if any, hunting played a role. It does appear that tool use played a role in this niche, and perhaps fire as well. While the evidence for early *Homo erectus*' foraging is meager, there is clear evidence that *Homo erectus*' geographic distribution expanded relative to that of earlier hominids. Recent dating of the Dmanisi mandible places *Homo erectus* in eastern Europe by at least 1.6 million years ago (Gabunia and Vekua, 1995). This expansion suggests that a significant change in niche had occurred; we are just not in a position to describe this niche in detail. At our present state of knowledge we can only accept that there was a temporal correlation between niche change, geographic expansion, and a real, if not dramatic, development in spatial cognition. However, developments in spatial cognition did not include those which demonstrate the most significant sex differences in modern humans.

A second significant development in foraging and ranging occurred late in the Palaeolithic when specialized collector subsistence systems made an appearance and when humans colonized hostile (Siberia, for example) and remote environments (Australia and the Americas). Specialized collectors focus on a narrow range of resources and often employ sophisticated technologies, such as long-term storage. Mass kills of single species are often an element in the hunting strategies of such groups. Prior to the Upper Palaeolithic of Eurasia and the Later Stone Age of Africa, humans appear to have operated closer to the forager end of the continuum, relying on a broad range of gathered, hunted, and scavenged resources. Coincident with the appearance of more specialized foraging, people expanded into much more hostile environments, like that of Beringia during the Late Glacial Maximum. These developments make a significant contrast with what preceded them, but on the time scale of human evolution they occurred very late, certainly after 100,000 years ago, and perhaps not until after 50,000. This was long after evidence for modern spatial abilities.

Between the advent of *Homo erectus* and the appearance of specialized collecting systems, there were certainly developments in hominid foraging, but none correlate well with developments in spatial cognition. It appears likely, for example, that hunting gradually came to play a more important role in foraging. We have convincing evidence for hunting at Hoxne (England) by perhaps 300,000 years ago (Singer et al., 1993). But scavenging continued to play an important role, even in the foraging of Neanderthals (Kuhn, 1993). Nowhere in the Palaeolithic can we identify a clear "advent of hunting," so we cannot make the convenient conclusion that hunting and spatial thinking were somehow related. Similarly, hominid distribution expanded, at least slightly, after 1 million years ago, to include western Europe. However, this was too early to provide some selective reason for sophisticated abilities in mental rotation.

Group range presents a similar picture. Even the earliest stone knappers appear to have had a larger group range than modern chimpanzees; at least one Oldowan hominid carried a chunk of gneiss 13 km. Early *Homo erectus* in East Africa commonly carried raw material 15–20 km (Cachel and Harris, 1995). By the time of Archaic *Homo sapiens*, individuals carried high quality flint up to 100 km (Roebroeks et al., 1988), and one group of Paleoindians (about 11,500 BP) in North America carried high quality raw material over a distance of 485 km (Meltzer, 1993). There *may* have been an increase in group range associated with the evolution of *Homo sapiens*, but the evidence is insufficient to make this conclusion with any confidence. Moreover, temperate latitude species almost always have larger ranges (and wider niches) than their tropical cousins, so any increase in *Homo*'s group range associated with movement out of the tropics is entirely predictable, and therefore not necessarily tied to spatial thinking.

CONCLUSION

Having reviewed the evidence for the neurological basis of the sex differences and the archaeological evidence for the timing of major evolutionary developments in spatial cognition, we are in a position to revisit the four

hypotheses presented earlier in this article. For one of these hypotheses to be persuasive it must succeed at three tasks. First, the documented sex differences in performance must fit the postulated selective pressures. Second, selection must have been able to work by means of the timing of prenatal hormones, testosterone in particular. Third, the hypothesis should be compatible with the paleoanthropological record. Ideally, there should be evidence that the character in question appeared in the archaeological record coincident with (or soon after) the proposed selective pressures.

The male hunting hypothesis fails to meet the first and third of these requirements. This hypothesis rests largely on the unsupported assumption that advanced spatial concepts play a role in hunting, especially in the use of projectiles. However, the most salient of the spatial abilities with a sex difference is mental rotation, and there is no reason to suppose that this ability affects projectile use in any way. Spatiotemporal ability also demonstrates a sex difference, and is arguably important when throwing projectiles at moving targets. The problem here is that hunters, with few exceptions, avoid aiming at moving targets; even with high-powered rifles, moving targets are difficult to hit. The evolutionary result—sex differences in spatial thinking—cannot be convincingly connected to the proposed selective agent, in this case hunting. The hypothesis also fails the test of evolutionary timing. Archaeological evidence indicates that projectiles appeared late in human evolution, and projectiles effective enough to intercept moving targets appeared very late indeed, long after convincing evidence for modern abilities in mental rotation, spatial perception, and spatial visualization. There is always the remote possibility that hunting with aimed projectiles appeared very early in human evolution, but that it left no archaeological traces. However, in arguing for the evolutionary advent of a significant behavior virtually unknown in other primates, we feel it is necessary to take a conservative stance. In these cases absence of evidence is, *a priori*, a strong argument for absence of the behavior. Another version of the hunting hypothesis stresses navigation skill. This makes a

better connection to spatial thinking than projectiles, but cannot account for the sex difference; presumably female foragers living in mobile and migratory bands also had to navigate.

The female forager hypothesis fails to meet any of the criteria for a convincing hypothesis. First of all, the sex difference itself is ambiguous. When Eals and Silverman used tests of “uncommon” objects they found mixed results between the recall abilities of males and females. A test based on memorizing drawings “of uncommon objects showed the same significant sex difference in location memory favoring females as did the same test with common objects. . . . Sex differences for object memory, however, also favored females but did not achieve significance” (1994:103). Even greater ambiguity was found in a more natural setting test involving directed and incidental memorizing of uncommon objects in an office: “A diverse trend was observed for uncommon objects. . . . For object memory scores, the only significant difference was contrary to the hypotheses; male scores were higher in the directed learning condition. Results for location memory, on the other hand, provided partial support for the hypotheses; females were significantly higher in the incidental learning condition only” (1994:103). The conclusion drawn from this evidence by Eals and Silverman is that “the most parsimonious interpretation incorporating all of the data is that for unfamiliar objects, the female advantage occurs solely for location memory in incidental learning conditions” (1994:103). Despite these limited results they continue to support an adaptationist explanation: “Based on their ancestral roles as food gatherers, keepers of the habitat, and caretakers of the young, the attentional styles of females may have evolved as more inclusive of the environment than males” (1994:103).

The above statement falls far short of a demonstration of a trait being designed by natural selection to fulfill a certain function. A “more inclusive attentional style” is a very vague “trait” indeed, and it is certainly not clear that the activities of females during the proposed period were significantly different in regard to environmental aware-

ness from the selective pressures on the spatial abilities of males who were presumably also engaged in considerable foraging activities.

It is also very difficult to accept that a female advantage in spatial cognition could have been selected by means of the timing of hormones in male fetuses, so the hypothesis fails to meet the second criterion. The proposed selective advantage cannot be connected to the evolutionary result via the proximate link of fetal hormone timing.

Finally, the female forager hypothesis sinks in the face of the evolutionary evidence. Foraging for plants hidden in complex backgrounds has always been part of primate niches, and foraging for buried foods may well have been part of the early hominid niche. Interestingly, there is considerable evidence for sex differences in the foraging patterns of non-human primates, including chimpanzees (Goodall, 1986; McGrew, 1992). Most primate foraging would benefit from the kinds of pattern discrimination tested in spatial visualization experiments. In other words, the selective agent proposed by Eals and Silverman has been in place for a very long time. There is certainly no reason to believe that the advent of a unique pattern in division of labor occurred in the hominid line until very late. In fact, the picture of hominid foraging advocated by Eals and Silverman—male specialized hunting and female generalized gathering—applies to *some* modern groups but is almost certainly an inaccurate description of the majority of the human past. Finally, the archaeological evidence for the kind of spatial visualization tested in the sex difference literature is inconclusive, but the ability appears to have evolved long before there is any evidence for modern foraging. The evolutionary timing just does not support a female foraging hypothesis.

The third adaptationist hypothesis, that of male reproductive strategy, fares better in the face of evidence than the hunting and foraging hypotheses. It is *a priori* a stronger hypothesis because it has successfully explained the sex differences in spatial cognition found in several non-primate species. It also fits the first two requirements for a persuasive hypothesis. Spatial concepts

such as mental rotation and spatial perception (frame dependency) could well enhance the “image of spatial organization” employed by males in their strategy of finding mates. Certainly, closely related primates (e.g., chimpanzees) employ boundary maintenance as an aspect of their reproductive strategy, and cognitive abilities that enhance one’s concept of territory might well enhance reproductive success. This hypothesis, then, provides a believable connection between the general characteristic and the selective agent, and incorporates a sex difference in selective agency (unlike general navigation hypotheses, for example). It can also incorporate selection by means of the timing of prenatal hormones, because there would be direct selection for male abilities by way of the timing of male fetal development.

The reproductive strategy hypothesis does not, however, do as well when placed against the archaeological record. There is convincing evidence for greater laterality of function for early *Homo*, who was predominantly right handed (Toth, 1985a). Increased laterality must have been a consequence of the same developmental mechanism (prenatal hormones) as sex differences in spatial cognition. Moreover, evidence of raw material transport indicates that the range of early *Homo* was almost certainly larger than that of any living ape (Wynn and McGrew, 1989). Yet at this point in the archaeological record (ca. 2 million years ago) there is no evidence for spatial abilities any different from those of an ape. In other words, there is evidence for the hypothesis’ selective agent (change in ranging behavior) and even some evidence for a corollary consequence (laterality), but no evidence for more powerful spatial thinking. Better support for the hypothesis is provided by *Homo erectus*. Early *Homo erectus* demonstrates a significant niche change, compared to earlier hominids, including early *Homo* (Walker and Leakey, 1993; Harris and Cachel, 1995). This niche change included a much increased group range. There is also evidence for the use of slightly more powerful spatial concepts, including rudimentary notions of spatial quantity. However, the spatial concepts for which there are modern sex differences, such as mental rotation, are not evident until long after the

advent of *Homo erectus*. Modern spatial thinking, including the abilities with sex differences, appear in the archaeological record coincident with the encephalization marking the evolution of Archaic *Homo sapiens*. There was not, however, any clear change in ranging behavior associated with this transition, though one occurred much later with the geographic expansions of the late Pleistocene.

Although Gaulin and Hoffman, the proponents of the reproductive advantage hypothesis, acknowledge that some traits "might not be an adaptation at all, but rather, an incidental side-effect of selection for some other trait" (1988:131), they fail seriously to consider that sex differences in spatial ability may be such a "side-effect." Their evidence, however, fails to rule out this possibility. Although cross-species comparisons may provide evidence of adaptation in a particular species, such evidence is rarely conclusive (see Crawford and Galdikas, 1986; Palmer, 1989). Furthermore, the timing of male-biased spatial abilities at adolescence is no more compatible with their adaptation hypothesis than it is with the hypothesis that it is simply the by-product of hormonal changes occurring at that stage of development for different reasons. Finally, the evidence on home ranges among contemporary societies is very limited and of varying usefulness as models for the home ranges of ancestral humans. Pertinent to this point is the fact that some studies of hunters and gatherers have failed to show the same significant sex differences in spatial ability found in other societies:

In a comparison of Baffin Island Eskimo hunters and West African Temne agriculturalists, Berry (1966) found the usual sex difference in the latter society, *but no statistically significant sex differences among the Eskimo*. He attributed his findings to the different life styles of the two groups. Among the Eskimo, whose hunting economy and dispersed settlement pattern require much travel, the ability to make subtle visual discriminations in a relatively featureless (undifferentiated) environment was thought to be critical to survival for both men and women. . . . In further cross-cultural work, Berry (1971:133) expanded on his initial ecological model, arguing that among traditional hunter-gatherer peoples, the possession of good visual discrimination and spatial skills is a necessity [1988:141; emphasis added].

Berry's finding, although far from conclusive, suggests that the selective pressures on the spatial abilities of males and females may be nearly equal in highly mobile hunting and gathering societies. This may be consistent with the expectation that among migratory species the breeding ranges of both males and females are minute compared to the size of their annual range. This annual range, which is often very similar for the two sexes, is probably more important in selecting for navigation skills, and its effects could overshadow any consequences arising out of sex differences in breeding range (1988:133). This is of obvious importance to hypotheses about the evolution of spatial abilities in humans because our ancestral populations were undoubtedly highly mobile gatherers, before and after the advent of hunting.

Although they may eventually be demonstrated to be accurate, the existing adaptationist explanations of male/female differences in spatial ability have not yet demonstrated sufficient evidence of design, nor do they fit with what we know of the evolution of spatial cognition. If one remembers that adaptation is an "onerous" concept that should only be invoked when other explanations can be ruled out, it becomes crucial to consider the possibility that male/female differences in cognitive abilities are simply by-products of other adaptive changes that have occurred during human evolution. Indeed, a by-product explanation becomes quite plausible when one examines both the proximate developmental causes of spatial abilities and the archaeological evidence indicating when these spatial abilities occurred during human evolution.

The sex difference in spatial cognition is an exemplary candidate for an evolutionary by-product. This is not simply a default position arising from the failure of adaptationist scenarios. There are compelling reasons for considering the difference to be a by-product. One is the abstract nature of the skills themselves. Carefully designed experiments can isolate a sex difference in rather arcane tasks such as "embedded figures" and "rotated blocks," but the few attempts to isolate a sex difference using real world problems have yielded ambiguous results, at best (Silverman and Eals, 1994; Alyman and Peters,

1993). The skills *may* play significant roles in the abstract world of mathematical reasoning (Benbow, 1988; Geary, 1996), but this can hardly have been a factor in human evolution. The cognitive skills tested in the sex difference literature just have not made very believable selective agents.

It is far more likely that selection operated strongly on the timing of fetal development. A change in the timing of certain fetal developments (such as those apparent in early *Homo erectus*? [Walker et al., 1993]) would affect the hormonal milieu of cerebral growth, including the effect of testosterone on cerebral asymmetry. It is easy to see how a change in the timing of fetal development could enhance or decrease the viability of the fetus, and by extension its later reproductive success (especially given the greater susceptibility of male fetuses to errors in development). Alternatively, selection could have worked through maternal viability; fetal hormonal timing that increased maternal well-being (vis-à-vis nausea and vomiting, for example) would presumably also be under selective pressure. In both of these scenarios, the timing of prenatal hormones could increase or decrease laterality of function in males as a by-product. Any sex difference in abstract spatial skills that appear much later in life would be purely accidental.

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